

DIET AND FUNCTIONAL MORPHOLOGY OF THE MANDIBLE
OF TWO PLANKTONIC AMPHIPODS FROM THE STRAIT OF GEORGIA,
BRITISH COLUMBIA, *PARATHEMISTO PACIFICA* (STEBBING, 1888)
AND *CYPHOCARIS CHALLENGERI* (STEBBING, 1888)

BY

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ABSTRACT

In amphipods, morphological adaptations for feeding provide taxonomic evidence that helps to differentiate them into species. Intuitively, this indicates that the morphology of feeding structures may be related to the type of food the amphipods consume. This hypothesis was examined using zooplankton collections from three locations from the Strait of Georgia, British Columbia: the Fraser River plume, the estuarine plume, and the Strait. The study investigated the mandible morphology, the stomach contents, and the potential food for the amphipods, *Parathemisto pacifica* and *Cyphocaris challengerii*.

Mandible morphology obtained with SEM photography and morphometric analyses was used to infer feeding habits. The mandible of *P. pacifica* has a wide molar indicative of microphagous habits and a cutting incisor related to carnivorous habits, while in *C. challengerii*, the strong molar and sharp incisor in the mandible indicate carnivorous habits. Stomach contents indicated that both *Parathemisto pacifica* and *Cyphocaris challengerii* preyed most frequently on copepods, amphipods, cladocerans, and ostracodes. The amphipods appeared to select female copepods, perhaps either because females can have a higher nutritious value when bearing eggs or because they are more abundant than male copepods. The difference in the diet between the two species was that amphipods were more abundant in stomachs of *C. challengerii* and copepods were more numerous in the stomachs of *P. pacifica*. The presence of small copepod species in the diet of amphipods suggests amphipods are an important link between nanoplankton, the food of copepods, and the fish that consume amphipods (e.g., salmonids and clupeids).

ZUSAMMENFASSUNG

Anpassungen im Zusammenhang mit der Nahrungsaufnahme sind bei Amphipoden eine Hilfe bei der Artabgrenzung. Rein intuitiv zeigt dies, dass eine Beziehung bestehen kann zwischen dem Bau der Nahrungsaufnahmegorgane und der Art der Nahrung, die von den Amphipoden konsumiert

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wird. Zur Prüfung dieser Hypothese wurden Zooplanktonproben von drei Standorten der Georgia-Straße, British-Columbia, untersucht: aus der Fahne des Fraser Flusses, der Mündungsfahne und der Georgia-Straße. Untersucht wurden der Bau der Mandibel, der Mageninhalt und die potentielle Nahrung der Amphipoden *Parathemisto pacifica* und *Cyphocaris challengerii*.

Rasterelektronenmikroskopische Aufnahmen der Mandibel und morphometrische Analysen wurden benutzt, um auf Nahrungsgewohnheiten rückzuschließen. Die Mandibel von *P. pacifica* hat eine breite pars molaris, die auf Mikrophagie hindeutet, und eine Schneidekante, die eher fleischfressende Gewohnheiten nahelegt. *C. challengerii* dagegen scheint mit seiner kräftigen pars molaris und scharfen Schneidekante der Mandibel ein richtiger Fleischfresser zu sein. Die Mageninhaltsuntersuchungen zeigten, dass sowohl *Parathemisto pacifica* als auch *Cyphocaris challengerii* hauptsächlich Copepoden, Amphipoden, Cladoceren und Ostracoden erbeuten. Beide scheinen Copepoden-Weibchen zu bevorzugen, entweder wegen ihres höheren Nährwerts, wenn sie Eier tragen, oder weil sie die Männchen an Zahl übertreffen. Der Unterschied in der Nahrung beider Arten bestand darin, dass der Magen von *C. challengerii* mehr Amphipoden und der von *P. pacifica* mehr Copepoden enthielt. Die Tatsache, dass kleine Copepoden-Arten zur Nahrung von Amphipoden gehören, legt nahe, dass diese ein wichtiges Bindeglied zwischen dem Nanoplankton, von dem sich die Copepoden ernähren, und Fischen sind (z.B. Salmoniden und Clupeiden), die Amphipoden verzehren.

INTRODUCTION

Amphipods are abundant in cold environments (Bowman & Gruner, 1973), particularly in highly productive, estuarine areas (Nair et al., 1973) as the Strait of Georgia, British Columbia (St. John et al., 1992). They can be an important part of the diet of whales (Nemoto, 1970) and fish (Birtwell et al., 1984; St. John et al., 1992), including salmon (Beacham, 1986; Brodeur, 1990), and keen zooplankton predators as well (Sheader & Evans, 1975). Knowledge of the feeding habits of amphipods can provide a better understanding of the role they play in the trophic ecology of the Strait of Georgia estuary.

The study reported here was based on the hypothesis that, because of environmental adaptations, there is a strong relationship between morphology and ecological characteristics (Reilly & Wainwright, 1994). The morphology of the mandible, and of the rest of the feeding appendages, is widely used for taxonomic classification of amphipods (Barnard, 1958) and the variation across species has proved quite useful in phylogenetic research (Watling, 1993; Bousfield, 1995). Yet, only a handful of studies has focused on the connection between morphology of oral appendages and ecology (e.g., Sainte-Marie, 1984; Moore & Rainbow, 1989; Coleman 1991a, b; Steele & Steele, 1993).

The premise was that the morphology of the mandible and feeding habits are closely related. Testing this hypothesis involved investigating the mandible morphology and stomach contents of the amphipods, *Cyphocaris challengerii* Stebbing, 1888 and *Parathemisto pacifica* Stebbing, 1888, species abundant in plankton collections from the Strait of Georgia. The study devoted particular attention to the mandible morphology because, among the mouthparts of amphipods, the mandible

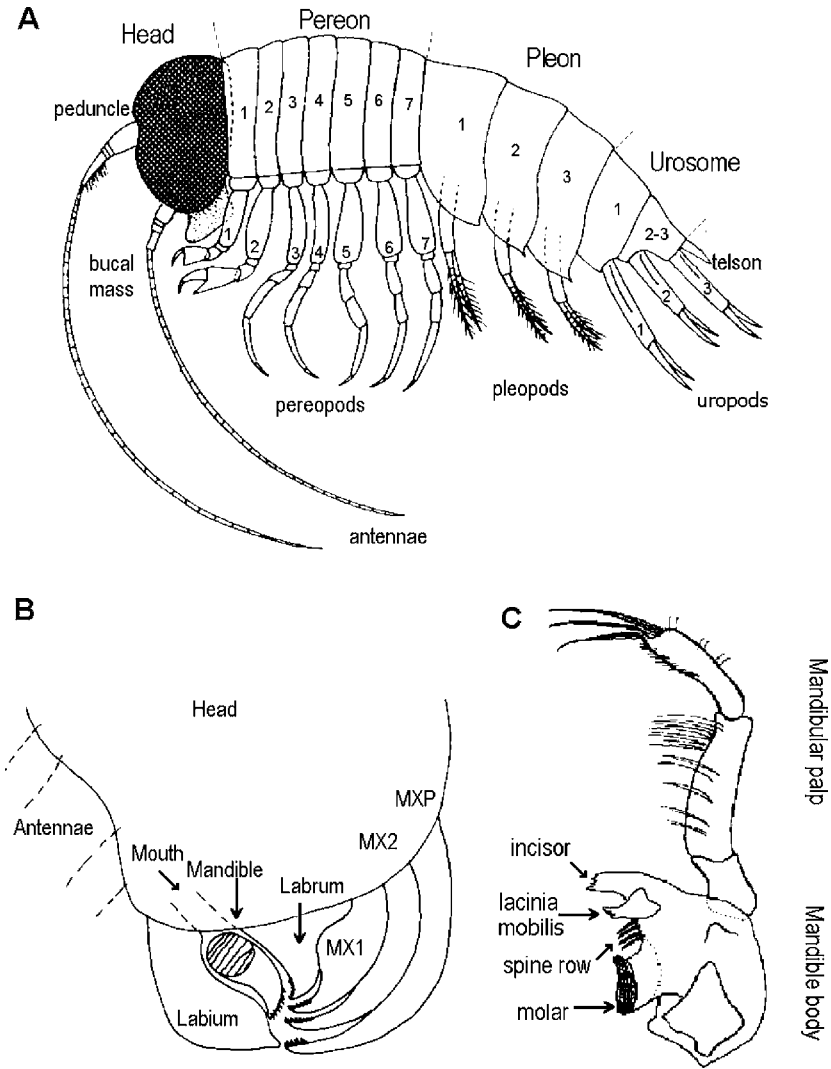


Fig. 1. Schematic representation of an amphipod: A, body parts; B, head showing mouthparts (MX1, maxilla 1; MX2, maxilla 2; MXP, maxilliped); C, mandible. [A, Redrawn from Bowman & Gruner, 1970; C, redrawn from Schmitz, 1992.]

has the greatest interspecific variation in shape, which can be related to feeding habits (Watling, 1993).

The mandible of amphipods is located ventrally on the head, in the bucal mass (fig. 1A). The bucal mass contains one pair of mandibles, two pairs of biramous maxillae, and one pair of basally fused maxillipeds (fig. 1B). The mandibles, the maxillae, and the maxillipeds each bear a palp (Bousfield, 1973) except in

hyperiids, which lack the palp in the maxilliped (Bowman & Gruner, 1973). The basic mandible of amphipods (fig. 1C) consists of a compact coxa or mandible body, bearing a toothed incisor, a lacinia mobilis, a row of setae leading dorsally to a molar designed for crushing, and a 3-article palp (Manton, 1977; Watling, 1993). Parts most susceptible to change are the incisor and the molar. The changes can include a reduction of the incisor, loss of the seta row, reduction or loss of the molar, or all of these (Watling, 1993).

The objective of this study was to investigate the mandible morphology of *P. pacifica* and *C. challengerii* in order to make inferences on what type of food they may be able to consume. Then, their stomach contents were analysed to verify what they were actually eating. The mandibles of *P. pacifica* and *C. challengerii* were previously described in drawings by Bowman (1960) and Barnard (1958), respectively. However, such descriptions do not include information on the functional morphology or the morphometrical changes the mandible undergoes during growth. This information was considered fundamental to show what type of food the mandible would enable these animals to eat and whether mandible shape changed during growth. Also, stomach contents of both amphipod species were identified to investigate what the animals were actually eating.

MATERIALS AND METHODS

Amphipods were obtained from zooplankton samples collected in the Strait of Georgia, British Columbia (fig. 2). Samples were collected during 1990 and 1991, in oblique hauls from 0-15/25 m depth with bongo nets of 296 μm and of 300 μm mesh size (Clifford et al., 1990, 1991a, b, 1992; Harrison et al., 1991). From these samples, 32 *Parathemisto pacifica* and 38 *Cyphocaris challengerii* individuals (figs. 3A, B) were selected covering a size range from 2 to 16 mm. The mandibles were dissected under a stereoscopic microscope, and then immersed in a drop of corn syrup mixed with formalin (Pennak, 1978). Mandible dimensions were measured using an inverted microscope and a camera lucida. The description of cuticular extensions of the mandible, such as spines and setae, follows the terminology proposed by Watling (1989).

For *Parathemisto pacifica* the measurements taken to examine the mandible morphometry were length and height of the molar, height and length of the cutting area of the incisor, and number of teeth in the incisor. For *Cyphocaris challengerii*, the length and height of the molar; the incisor height, length of the incisor cutting area, and length of the incisor base were taken. In order to identify changes in the mandible structure during growth, all dimensions were regressed

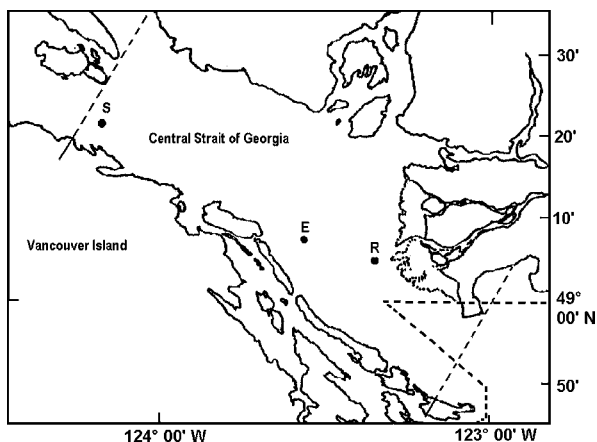


Fig. 2. Area of study: the central Strait of Georgia. R, E, S, and DFO1 are the sampling stations in this study: R, riverine plume; E, estuarine plume; and S, Strait.

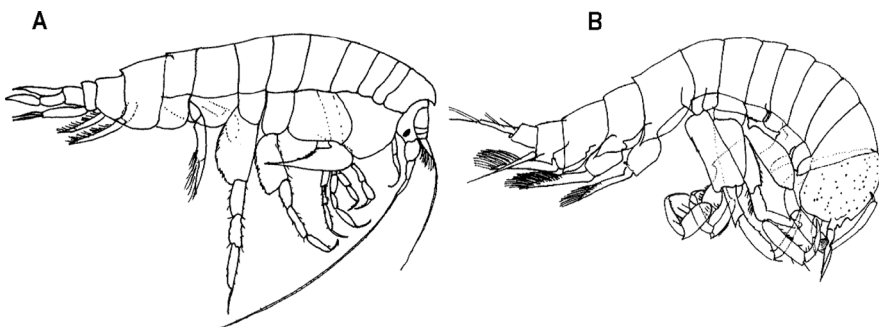


Fig. 3. Amphipod species studied. A, *Cyphocaris challengerii* Stebbing, 1888 (adult, approx. 12 mm); B, *Parathemisto pacifica* Stebbing, 1888 (adult, approx. 10 mm).

against body size. Selected images of the mandibles were obtained by scanning electron microscopy. Preparation for scanning microscopy consisted of a series of alcohol for dehydration, critical point drying with CO_2 , and gold coating. Electron microscopy was performed in the UBC Botany-Zoology Electron Microscopy laboratory, with a conventional scanning electron microscope Zeiss EM 10c SEM.

Stomach contents were emptied onto glass slides and examined under an inverted microscope. These contents were separated into pieces, and the appearance of each particle was recorded with as much detail as possible (e.g., round, small particles, spines, cuticle pieces, brown material, etc.). Food items found intact were measured and identified to the nearest taxonomic level according to criteria of selected literature. The size of complete prey items was plotted against the size of the animal in which they were found.

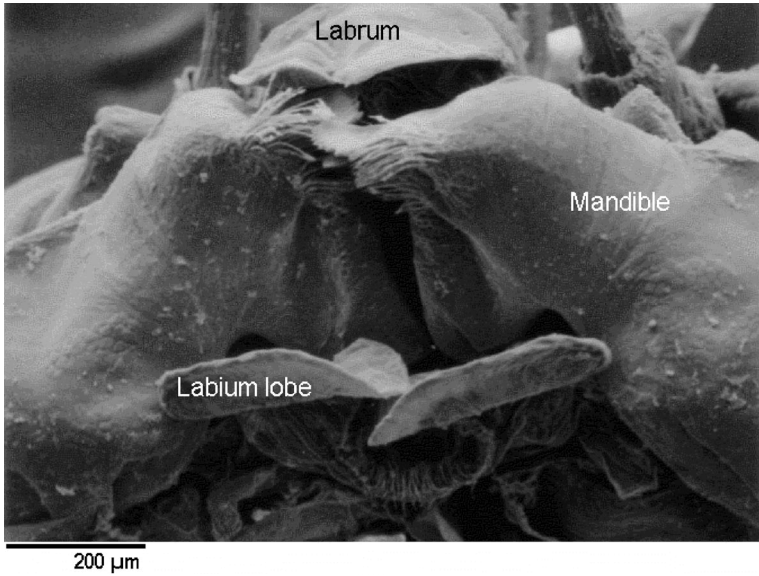


Fig. 4. Scanning electron microscope image of *Parathemisto pacifica* Stebbing, 1888 mandibles.

RESULTS

The mandible of *Parathemisto pacifica*

The mandibles are elongated, have a thin integument, insert laterally on the head, and meet frontally under the labrum. The mandibular palps are directed frontally on both sides of the labrum (fig. 4). The labrum has a medioapical notch that covers the dorsal areas of the mandibles and partially overlaps them. The labium is bilobate, each lobe is oval and wide (fig. 4). The mandibles fit between the labrum and the labium (fig. 4), and surround the mouth. The incisors are wide and toothed, and laterally flanked on the external edge with a brush-looking set of long setae (fig. 5). The teeth are sclerotized. Only the left mandible has a lacinia mobilis, which is about 30% smaller than the incisor and is similarly toothed. The left mandible embraces the right one between the incisor and the lacinia mobilis when closed. The distal tooth on the left mandible fits between the two distal teeth of the right mandible. The molar arises from the frontal part of the mandible. It is broad and round in small specimens, and elongated and lanceolated in large specimens. Its surface is covered with rows of lamellae with blunted, sclerotized ridges (fig. 6). The molar has a fringe structure, with longer setae on the internal margin than those on the external margin. Between the molar and the incisor process, a small group of sharp setae protrudes forming the seta row (figs. 5-6).

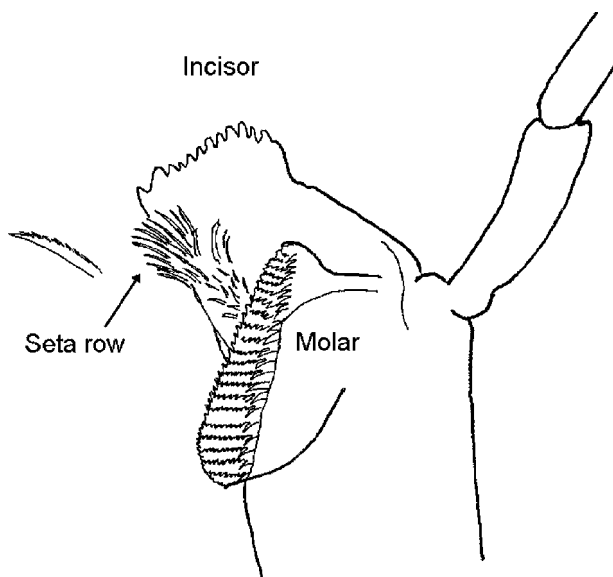


Fig. 5. Schematic representation of *Parathemisto pacifica* Stebbing, 1888 left mandible showing the incisor, molar, seta row, and a detail of a seta.

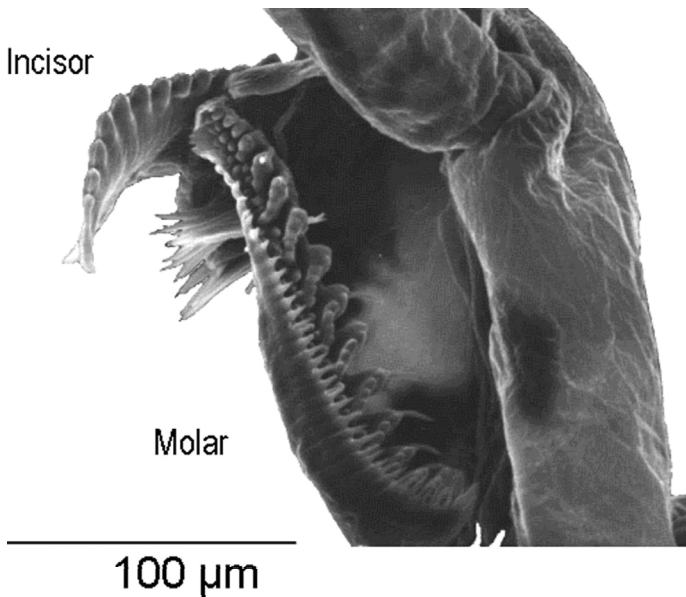


Fig. 6. Scanning electron microscope image of *Parathemisto pacifica* Stebbing, 1888 mandible. Note the lamelliform rows with blunt cusps on the molar.

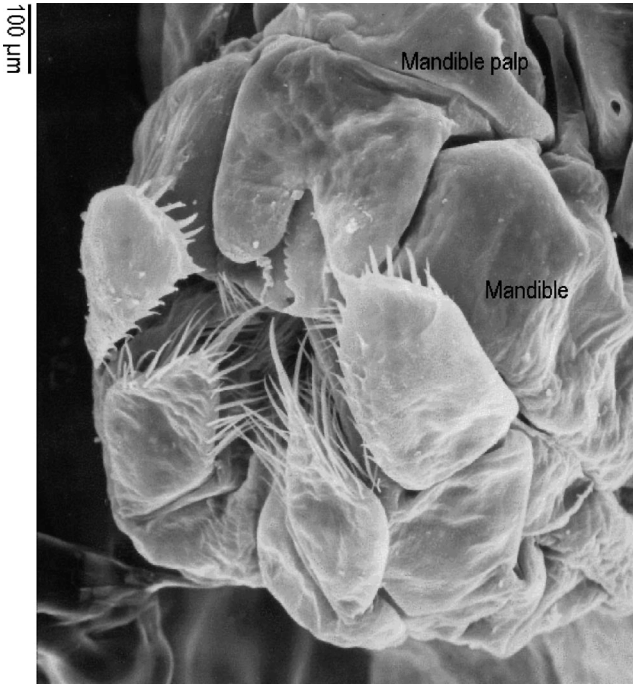


Fig. 7. Scanning electron microscope image of *Parathemisto pacifica* Stebbing, 1888 mouthparts showing the mandible and the mandible palp.

Function of the mandible of *Parathemisto pacifica*

The frontal disposition of the incisors and their toothed cutting edges indicate they work as a pair of trimming scissors. Food may cling on the setae flanking the external edges of the incisors during the cutting action, and is pushed further inside mechanically with the next bite. The medioapical notch of the labrum allows the use of the anterior incisor regions to produce a wide bite in which the right mandible crosses between the incisor and the lacinia mobilis of the left mandible in a cutting fashion. The insertion of the distal tooth of the left incisor between the pair of distal teeth of the right one suggests that when the mandibles close, the incisors come together in a clasping action, for trimming and cutting. The row of setae adjacent to the incisor grasps and directs the food towards the molars. While the incisors preferentially function for cutting, the molars grind the food. The surface area of the molar process is slightly sclerotized. During feeding, the long, sharp spines of the maxillipeds and the palps of the first maxillae point to the mouth area (fig. 7), which helps in handling the food, thus facilitating the work of the mandibles.



Fig. 8. The labrum of *Cyphocaris challengerii* Stebbing, 1888.

The mandible of *Cyphocaris challengerii*

The mandibles are slender and elongated, with a strong integument; they insert laterally on the head and meet frontally under the narrow apex of the labrum. The labrum is small, flattened, and drop-shaped with a frontal apex (fig. 8). It only covers the proximal parts of the incisors. The labium is triangular and bilobate. The mandibles fit between the labrum and the labium, with the mouth located above the mandibles (fig. 9). The incisors are toothless, axe-like, and sclerotized. The lacinia mobilis is columnar, narrow, toothed, and present only on the left mandible (fig. 10). When the mandibles close, the left mandible embraces the right

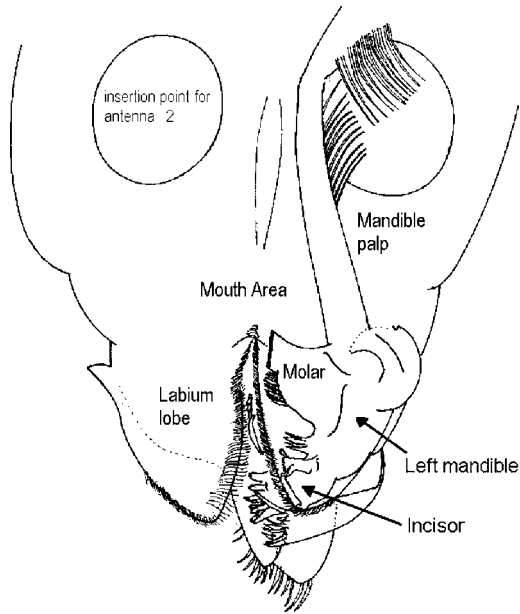


Fig. 9. Schematic representation of *Cyphocaris challengeri* Stebbing, 1888 left mandible showing its position with respect to other mouthparts.

one between the right incisor and the lacinia mobilis. The seta row between the incisor and the molar is composed of 6 long, strong setae that bear small serrations. The molar is cuboid, compact, highly sclerotized, and fringed with bundles of fine setae along its internal margin. Its triturative surface consists of a regular pattern of ridges across the molar. The mandibular palps are strong, oriented frontally at both sides of the labrum, and operate both frontally and on the basal area of the antennae.

Function of the mandible of *Cyphocaris challengeri*

The incisors are frontally oriented and their toothless, axe-like cutting edges indicate they work as a pair of sharp scalpels. The mandibles fit between the labrum and the labium and meet in a narrow region under the apex of the shield-shaped labrum (figs. 8-9). This arrangement suggests limited opening, since the labrum shape and size determine the bite gap (Manton, 1977). During biting, the right incisor may glide between the left incisor and the lacinia mobilis, following a curved path that their wedge shape dictates. The distal indentation on the left incisor may be clasped onto the hook ending of the right incisor. The seta row adjacent to the incisor is composed of long and strong setae that seem capable of holding large pieces of food and directing them towards the molar. The space between the incisor and the molar is large and suggests a capability for handling

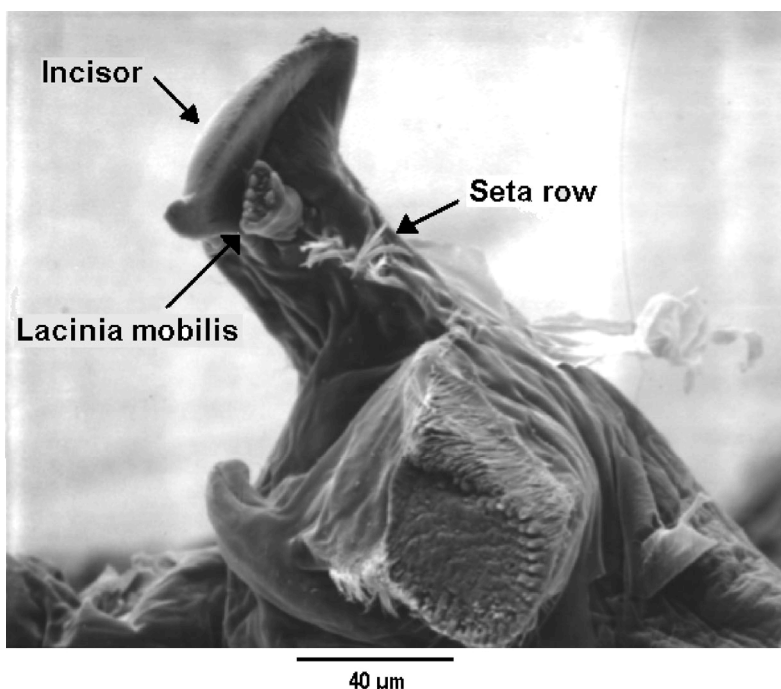


Fig. 10. Scanning electron microscope image of *Cyphocaris challengeri* Stebbing, 1888 left mandible.

relatively large pieces of food. When the mandibles close, the molars come together, presumably crushing the food between them. While feeding, the palps from the mandible and the maxillipeds meet on the mid-line, helping to hold the food for biting, or to prevent it from escaping. The long spines and the tooth-like spines of the proximal endite, all oriented medially, help to hold the food and to support and guide it towards the mandibles.

Morphometrics of the mandible of *Parathemisto pacifica*

The changes in dimension for the incisor and molar during growth are shown in figs. 11-14. The change in molar dimensions related to the body growth of *Parathemisto pacifica* is allometric in nature. The molar length shows a logarithmic relationship with body size. The molar length rapidly increases with body size from 2 to 7 mm and then remains almost constant for the remaining sizes (fig. 11). In comparison, molar height exhibits a slight increase in the 2-7 mm size interval (fig. 12), and beyond this size its height increases more acutely. In fact, the molar process changed shape throughout growth: in small specimens it is round and short, with a wide surface area that changes into a tall, columnar molar process with a slender and lanceolate surface area in large specimens. The number of teeth on the

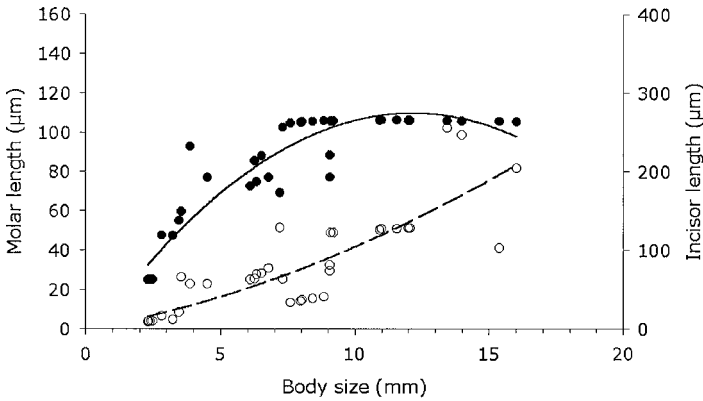


Fig. 11. Morphometric relation between body size and mandible characteristics of *Parathemisto pacifica* Stebbing, 1888. Molar length and body size (filled circles, continuous line) follow the relation $Y = 45.68 \text{ LN}(Y) - 4.088$ ($r^2 = 0.84$, $n = 38$). Incisor length and body size (open circles, dotted line) follow the relation $Y = 10.26 e^{0.214X}$ ($r^2 = 0.71$, $n = 38$).

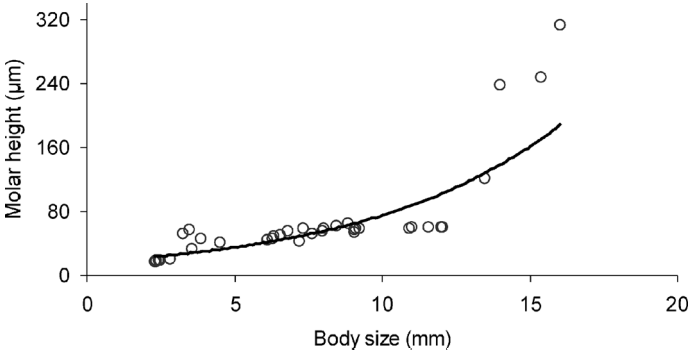


Fig. 12. Morphometric relation between body size and molar height of *Parathemisto pacifica* Stebbing, 1888. The trend line follows the relation $Y = 70.46 - 18.29X + 1.87X^2$ ($r^2 = 0.81$, $n = 38$).

incisor increases from 7 to 12 in the 2-5 mm size range organisms to 12 to 14 in >5-13 mm size range organisms; in organisms of 13 mm up to a maximum size of 16 mm, the incisor only acquires one more tooth, while the length of the incisor increases exponentially (fig. 13). Finally, the height of the incisor and the body size follow a quadratic relationship, suggesting allometry in the morphological change of the incisor during growth (fig. 14).

Morphometrics of the mandible of *Cyphocaris challengerii*

The dimensions of the molar and incisor processes increase linearly with body size (figs. 15-17), and only differ in how rapidly those dimensions change with the animal's growth. The height and the base of the incisor grow more slowly than do molar height and incisor length. This indicates that during growth, the

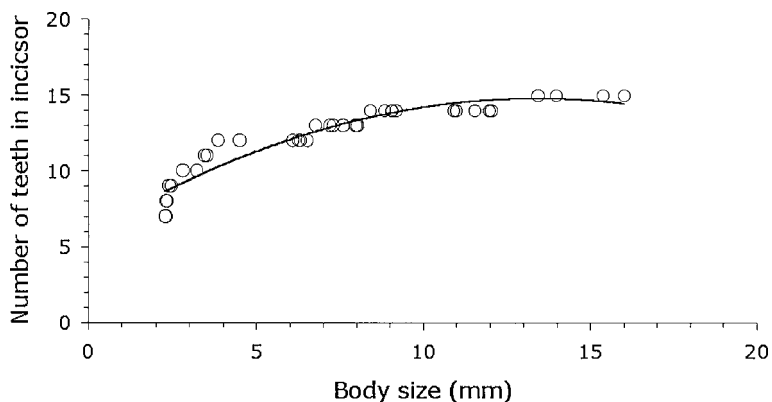


Fig. 13. Morphometric relation between body size and number of teeth in the incisor of *Parathemisto pacifica* Stebbing, 1888. Trend line follows the relation $Y = 3.637 \text{ LN}(X) + 5.573$ ($r^2 = 0.92$, $n = 38$).

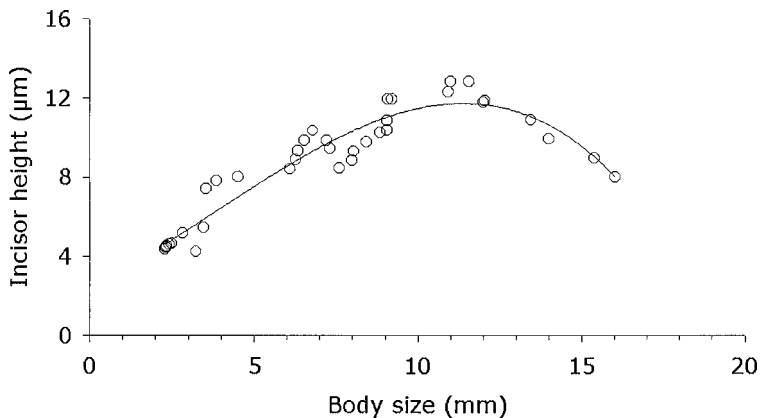


Fig. 14. Morphometric relation between body size and incisor height of *Parathemisto pacifica* Stebbing, 1888. Trend line follows the relation $Y = -0.093X^2 + 2.047X + 0.066$ ($r^2 = 0.90$, $n = 38$).

incisor widens while the molar process becomes shorter, narrower, and presumably sturdier. These relationships indicate that the change in mandible shape during the growth of *C. challengeri* is isometric.

Stomach contents

Five-hundred-and-sixty-five amphipods (307 *Parathemisto pacifica* and 258 *Cyphocaris challengeri*) were dissected and their stomach contents were analysed. Ingested prey was identified in about 50% of the stomachs dissected, 140 items were documented for *Parathemisto pacifica* and 116 for *Cyphocaris challengeri*.

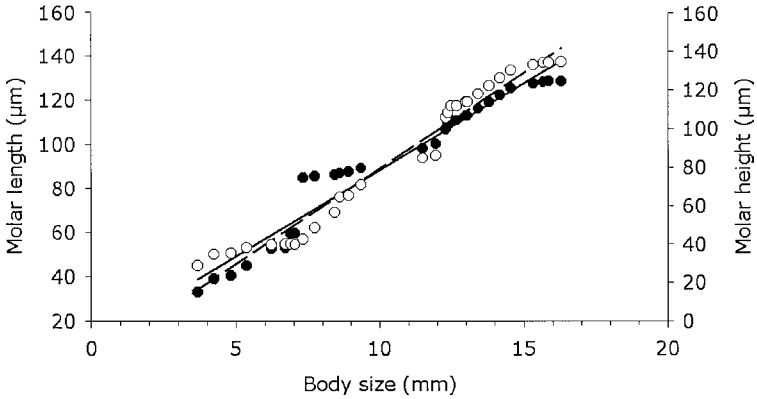


Fig. 15. Morphometric relation between body size and molar dimensions of *Cyphocaris challengeri* Stebbing, 1888. Molar length and body size (filled circles, continuous line) follow the relation $Y = 7.852X + 10.068$ ($r^2 = 0.95$, $n = 32$). Molar height and body size (open circles, dotted line) follow the relation $Y = 9.943X - 20.45$ ($r^2 = 0.96$, $n = 32$).

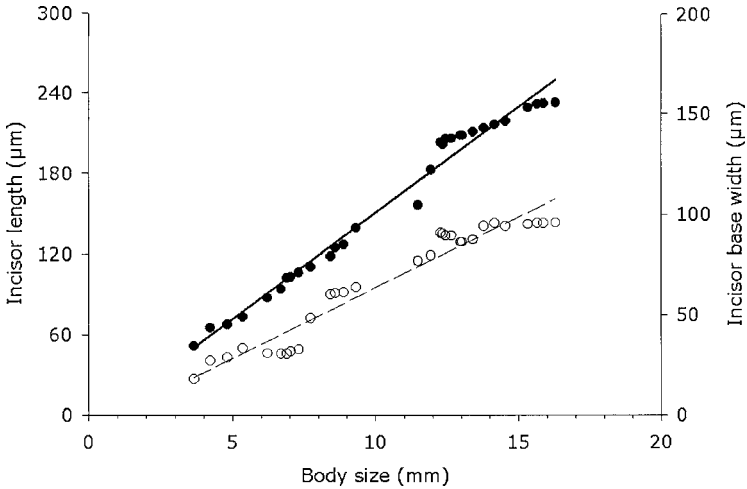


Fig. 16. Morphometric relation between body size and incisor dimensions of *Cyphocaris challengeri* Stebbing, 1888. Incisor length and body size (filled circles, continuous line) follow the relation $Y = 15.83X - 7.89$ ($r^2 = 0.98$, $n = 32$). Incisor base width and body size (open circles, dotted line) follow the relation $Y = 7.03X - 7.11$ ($r^2 = 0.93$, $n = 32$).

The most common groups identified in stomach contents were copepods, cladocerans, and ostracodes. Both amphipod species were frequently found to prey upon each other and even on their own species. Larvae of barnacles, bryozoans, crabs, and euphausiids were also present in the diet of both species, although less frequently, each accounting for less than 1% (and not shown in the percentage composition in figs. 16-17).

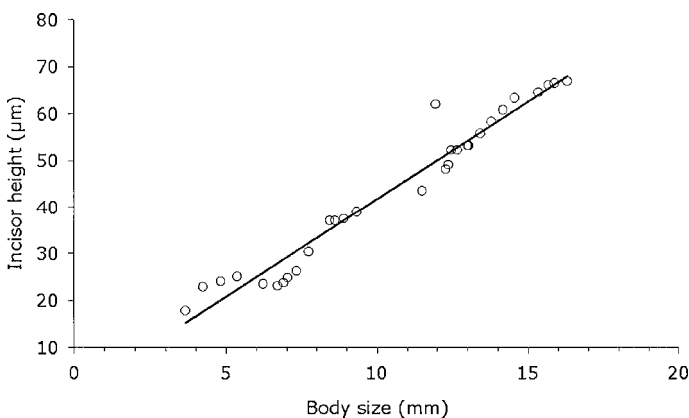


Fig. 17. Morphometric relation between body size and incisor height of *Cyphocaris challengerii* Stebbing, 1888. Trend line follows the relation $Y = 4.188X - 0.152$ ($r^2 = 0.95$, $n = 32$).

Stomach contents of *Parathemisto pacifica*

The stomach contents of *P. pacifica* contained small copepods, amphipods, cladocerans, ostracodes, crustacean larvae, diatoms, and euphausiids. Copepods composed 52% of their diet, followed by amphipods (33%) including *P. pacifica* itself and *C. challengerii*. The results of the size, frequency, and nature of the prey found in stomach contents suggest *Parathemisto pacifica* with body size from 2 to 12 mm (fig. 18A, B) primarily consume copepods. The size range in which they ingest ostracodes and the amphipod *C. challengerii* was from 3 to 9 mm.

The size range of the prey found in the stomach contents of *P. pacifica* was 0.3 to 3 mm (fig. 18B), with a mean prey size of 0.96 mm and a standard deviation of 0.58 mm. The size range of *P. pacifica* studied was from about 2 to 12 mm. Throughout its size range, *P. pacifica* ingested prey within the minimum prey size and progressively ate larger prey as its body size increased. Large and complete prey items were more frequently found in the stomach contents of individuals measuring 6 to 9 mm.

Stomach contents of *Cyphocaris challengerii*

Data suggested that *C. challengerii* ingested small prey throughout the size range studied (of 2 to 16 mm). *C. challengerii* ingested amphipods including their own youngsters, as well as *P. pacifica* (41%), copepods (33%), cladocerans, and ostracodes (fig. 19A). Bryozoa cyphonautes larvae and barnacle larvae were found in the stomachs of *C. challengerii* ranging from 8 to 14 mm, and diatoms were found in the stomachs of individuals ranging from 9 to 14 mm. Fig. 19B shows that the size range of the prey found in dissected stomachs of *C. challengerii* was 0.45-2.5 mm, with a mean size of 0.94 mm and a standard deviation of 0.39 mm.

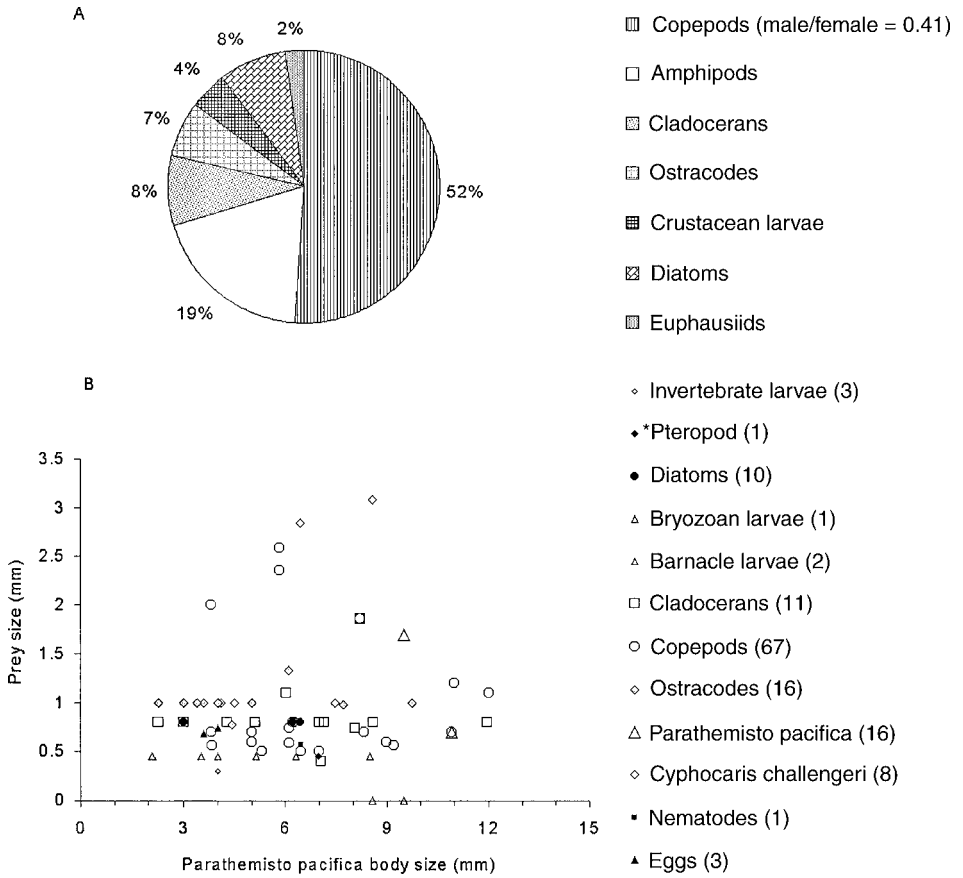


Fig. 18. A, Prey composition in the stomach contents of *Parathemisto pacifica* Stebbing, 1888; B, prey items identified at species or group level in 63 stomachs examined for *Parathemisto pacifica* Stebbing, 1888. The number of times the prey was found in stomach contents is given in parentheses. Prey size range was 0.3-3.0 mm, mean value = 0.96 mm, and standard deviation = 0.58 mm. *Pteropod: *Limacina helicina* Phipps, 1774.

As expected, the largest prey size present in the stomach contents increased at larger body sizes of *C. challengerii*, but what was mainly observed was an increase in the number of prey with growth.

DISCUSSION

Mandible morphology

The morphology of the mandible of *Parathemisto pacifica* and *Cyphocaris challengerii* exhibits similar elements. However, a closer look at the particular morphology of each species indicates functional differences in their action that

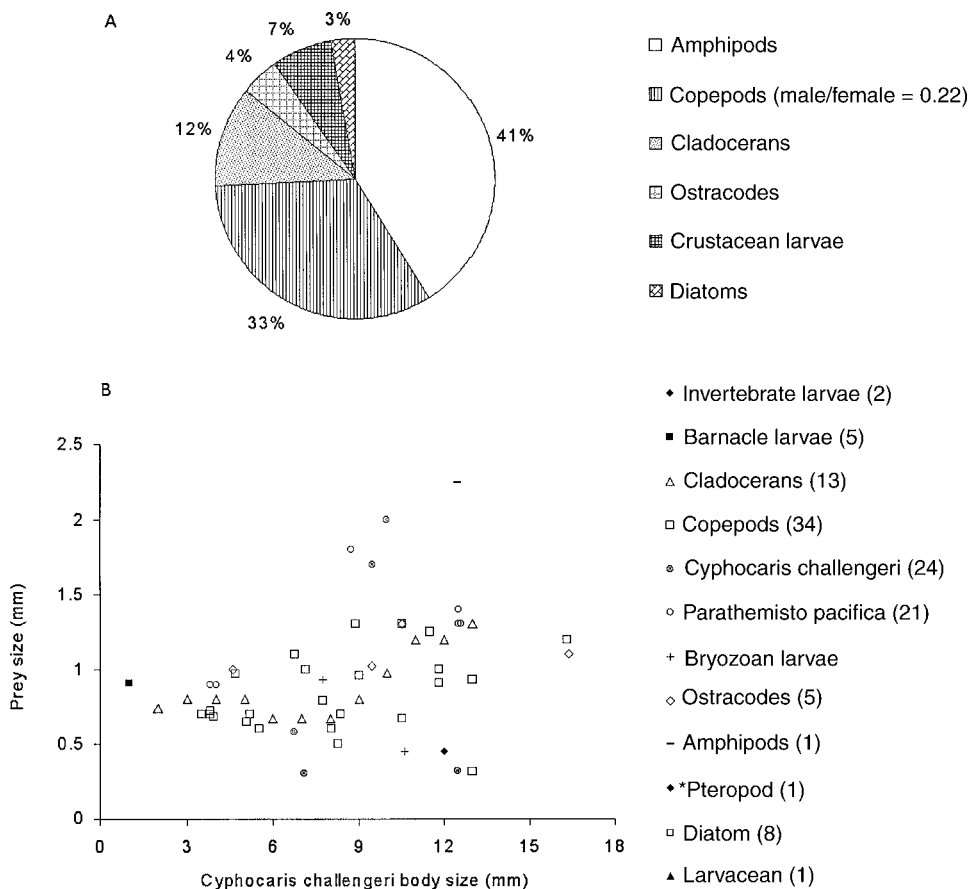


Fig. 19. A, Prey composition in the stomach contents of *Cyphocaris challengerii* Stebbing, 1888; B, prey items identified at species or group level in 57 stomachs of *Cyphocaris challengerii*. The number of times the prey found in stomach contents is given in parentheses. Prey size range was 0.45-2.5 mm, mean value = 0.94 mm, and standard deviation = 0.39 mm. *Pteropod: *Limacina helicina* Phipps, 1774.

presumably could affect what they eat and thus their trophic ecology. Literature on functional morphology of the mandible in amphipods relates a wide molar, similar to that present in *P. pacifica*, to herbivorous/microphagous habits (Watling, 1993), while the stout crushing molar of the gammaridean *C. challengerii* is related to carnivorous habits (Sainte-Marie, 1984). In both *P. pacifica* and *C. challengerii*, the mandible is elongate with the incisor at its front, which is generally associated with the ability to cut large pieces of food in carnivorous species (Watling, 1993).

Toothed incisors as those found in *P. pacifica* are present in hyperiids that feed on soft food (e.g., *Lestrigonus schizogeneios* Stebbing, 1888 and *Hyperietta stebbingi* Bowman, 1973). *L. schizogeneios* is known to feed on marine snow, and has also been found to burrow on the mesogloea of the medusa *Aequorea*

sp. (Harbison et al., 1977), which may indicate that it also feeds on gelatinous plankton. *L. schizogeneios* has a wide molar with blunt cusps (Bowman, 1973) similar to those found in *P. pacifica*. The molar of *H. stebbingi* is reduced compared to that of *P. pacifica*, and has sharp cusps on the molar surface (Bowman, 1973). This species feeds on egg masses and radiolarians (Harbison et al., 1977). By contrast, it may be inferred that the blunt lamelliform cusps found in the molar of *P. pacifica* serve for crushing masses of soft food, such as the organic matter found in marine snow, and perhaps also serve for breaking microzooplankton exoskeletons that may be present in marine snow or in particulate matter.

The ability of the mandibles to cut large pieces of food, the ample digestive chamber, and the tendency of hyperiids to feed on soft tissue found in gelatinous plankton (Laval, 1980) suggests this may be a food source for *P. pacifica*. However, the protected nature of the foregut, and evidence of raptorial habits in the related species, *P. gaudichaudii* (Guérin, 1825) (cf. Sheader & Evans, 1975), and the presence of a wide molar in *P. pacifica*, also suggest this species is capable of feeding on organisms with exoskeleton, and therefore possesses some raptorial capability.

The non-linear morphometric relationships between elements of the mandible of *P. pacifica* indicate that the change in mandible shape during growth is allometric. This suggests that the mandible capability and feeding habits of *P. pacifica* may change during growth. Young individuals have a wider molar than do adults, indicating perhaps an acute microphagy early in life, while the incisor of adults is wider and taller than that of small individuals, which is indicative of carnivorous habits.

The sharp, toothless incisor of *Cyphocaris challengerii* is commonly found in species belonging to the family Lysianassidae, and is considered an adaptation of carnivores for shearing-off large pieces of food (Steele & Steele, 1993; Watling, 1993). Lyssianasids with incisor-bearing mandibles but reduced or lacking molar processes have predominantly necrophagous habits and their stomachs contain large pieces of soft food (Sainte-Marie, 1984; Broyer & Thurston, 1987). On the other hand, big-sized scavengers observed to possess a vestigial molar (e.g., *Anonyx sarsi* Steel & Brunel, 1968; cf. Sainte-Marie & Lamarche, 1985), may exhibit some predatory activity. However, predation was limited to weak prey and only observed in large individuals with high swimming capability.

Strong palps and molars and sharp incisors on the mandibles of *Cyphocaris challengerii* are indicative of its predacious nature. Such mandible features enable them to access food from exoskeleton-protected, small planktonic invertebrates. In contrast, the comparatively weaker mandibular palps and toothed, comb-like incisors in *Parathemisto pacifica* seem indicative of a lesser predacious capability.

The morphometric relationships between elements of the mandible of *C. challengerii* are linear, indicating that the change in mandible shape during growth

is isometric. This suggests that as *C. challengerii* grows, there is an increase in mandible capabilities for crushing and cutting. This would allow them to feed on bigger food particles. It also suggests that *C. challengerii* is a carnivore throughout its life.

Stomach contents

Considering the mandibular elements observed in *Parathemisto pacifica*, it was anticipated that its diet might consist of detritus, small invertebrates, and soft tissue from coelenterates or perhaps fish larvae. The mandibular structure of *C. challengerii* suggested the type of food would include hard-shelled crustaceans and soft fish larvae as well. Stomachs of both species contained a varied assortment of small crustaceans, including their own species and each other's young. Diatoms were more abundant in *P. pacifica* stomach contents, perhaps indirectly from high consumption of copepods which feed on diatoms, or directly from the microphagous capability its mandible morphology indicates. That these two species have a somewhat overlapping diet may relate to the mandible morphology indicating carnivorous feeding in both species.

Stomach contents indicated that both *Parathemisto pacifica* and *Cyphocaris challengerii* most frequently prey on copepods, amphipods, cladocerans, and ostracodes. The prey was similar in size for both amphipods, with *P. pacifica* consuming prey over a somewhat wider size range. There was no evidence of a change of prey type consumed over the size range analysed, but the size of the same prey type and/or the number of prey did increase. The amphipods appeared to select female copepods, suggesting females as a preferred prey type, perhaps because females can have a higher nutritious value when bearing eggs, or simply because female copepods are far more numerous than males. The difference in diet between the two species was that amphipods were more abundant in stomachs of *C. challengerii* and copepods were more numerous in the stomachs of *P. pacifica*. Crustacean larvae were more abundant in *C. challengerii* than in *P. pacifica*, while euphausiids were found only in the stomach of *P. pacifica*.

What is missing is prey that may have been eaten but did not show up in the analyses. The type of prey most likely to be missing in the stomachs would include jelly-like food (e.g., coelenterates) or food that is rapidly digested (e.g., partially decomposed food). If this is the case for *P. pacifica* and/or *C. challengerii*, then the stomach contents analysis is providing a diet composition biased towards organisms with hard to digest or indigestible structures (e.g., crustaceans). The analysis of zooplankton diets using field samples can be biased towards the zooplankton species caught in the sample. Although the possibility of feeding during confinement could occur for some zooplankters, Shearer & Evans (1975)

observed that *P. gaudichaudii* specimens had to be exposed to prey for 3-5 days to accept it as a food source. Their results from both laboratory prey selection experiments and gut content analysis of field samples also indicated that a prey species was more likely to become their food if it had previously formed part of the diet of *Parathemisto*. This suggests that the stomach contents of *Parathemisto* are close to its true diet.

Finally, predominance of small organisms, particularly copepods (0.7 to 2 mm) in the diet of *P. pacifica* and *C. challengerii* indicate amphipods may serve as a trophic link between small mesozooplankton and bigger zooplankton consumers. In the Strait of Georgia, juvenile salmon and herring have been observed to feed in the Fraser River plume and estuarine plume areas (St. John et al., 1992). In particular, sockeye salmon have been observed feeding on *P. pacifica* both during juvenile and adult stages (cf. Beacham, 1986). Also large, juvenile pink salmon were observed to consume *P. pacifica* (cf. Beacham, 1986). Considering that type and quantity of prey may limit the survival of young fish (Lasker, 1975; Arthur, 1976), amphipods may benefit the fish species that prey on them by concentrating food energy and biomass from small zooplankton.

In summary, the feeding habits inferred from the shape and functional morphology of the mandible were reasonably close for both species, as the stomach contents indicated. Similarities in the diet composition are thought to derive from a shared carnivorous capacity in the amphipod species studied, although the shape and functional morphology of the mandible indicated different feeding strategy for each species. Exclusive carnivory and pelagic habits suggest *C. challengerii* is an active predator, whereas microphagy/carnivory suggests *P. pacifica* is a passive predator. This may also explain *C. challengerii* preying more intensively on *P. pacifica* than *P. pacifica* on *C. challengerii*.

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